

VARIATION IN MASS OF FEMALE PROTHONOTARY WARBLERS DURING NESTING

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ABSTRACT.—Over an 18-year period (1987–2004), we examined variation in body mass of female Prothonotary Warblers (*Protonotaria citrea*) captured throughout their nesting cycle. As is typical for many small passerine birds, body mass was greatest during egg laying and decreased throughout incubation and feeding of young. Mass decreased significantly between the onset of incubation and fledging of both first and second broods. Mass loss was gradual during incubation, noteworthy during the first 2 days of feeding nestlings, but did not continue to decrease throughout the feeding period. Mass lost while raising the first brood was regained before initiating the second brood. Mass of female warblers, adjusted for effects of nest attempt, year, clutch size, and day and stage of nesting, increased slightly with age. Body mass of nesting female warblers varied significantly with day of the nest cycle during incubation but not during egg laying or feeding of young. Mass was associated with clutch size during incubation in both first and second broods, but was not associated significantly with brood size when females were feeding nestlings. Frequency of food delivery to nestlings was associated negatively with female body mass. Females typically made more feeding trips per day than males. Feeding rates were correlated among pairs; that is, females with higher rates of delivery were mated to males that made a higher number of trips. Received 18 February 2005, accepted 21 October 2005.

Mass loss is often used as an index of reproductive costs in birds (see review in Merkle and Barclay 1996), largely because it is a consistent factor in patterns of avian life history. During the breeding season, female passerine birds typically gain mass in the period before egg laying, maintain or gradually lose a small amount during incubation, and then lose a significant amount of mass during brooding (e.g., Ricklefs 1974; Freed 1981; Moreno 1989a, 1989b). A similar pattern of change during breeding has been documented in several passerine birds (e.g., Freed 1981, Ricklefs and Hussell 1984, Hillström 1995, Merilä and Wiggins 1997). Researchers have hypothesized that mass loss may be a proximate response to energetic demands (e.g., Nice 1937, Hussell 1972, Askenmo 1977). Specifically, mass loss should be greatest during periods when energy demands are greatest, particularly near fledging when nestlings have acquired the ability to thermoregulate, and are relatively large. According to this hypothesis, mass loss should be a function of brood size. A second hypothesis suggests that decreased mass reduces the energy required

for flight when food demands of nestlings are greatest, thus reducing energy requirements of females and increasing the efficiency of feeding the young (e.g., Freed 1981, Norberg 1981, Hinsley 2000). In this instance, body mass should decrease shortly after eggs hatch and should be independent of brood size. A final hypothesis is that mass loss results from degeneration of female reproductive tissues during the nesting cycle (Ricklefs 1974, Ricklefs and Hussell 1984), and should not progressively occur during incubation or feeding of young. Some studies have eliminated the tissue degeneration hypothesis because gonadal atrophy is over before the period when mass loss is greatest (Moreno 1989a, 1989b; Merkle and Barclay 1996). It is difficult to isolate these three hypotheses, however, and some researchers have not found them to be mutually exclusive (e.g., Hillström 1995, Merilä and Wiggins 1997).

The question that usually has been addressed is: “Is mass loss evidence of energy demand and/or does it reduce costs of flight and enhance parental fitness?” It has been shown that energy expenditure is related significantly to rates of nest visitation, but not always in a linear manner (Bryant 1988). Furthermore, decreased body mass of adults rearing young may enhance their fitness through reduction of energy demand during the period of feeding nestlings. Our study examined

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measurements of body mass of female Prothonotary Warblers (*Protonotaria citrea*) obtained over an 18-year period. With these data, we attempted to answer three questions: (1) How does female body mass in this species vary over the breeding season? (2) Does body mass vary significantly among stages of nesting and among years? (3) What are the roles of brood size, stage of reproduction, and nest attempt in determining body mass in this species?

METHODS

Study area and measurement of mass.—Beginning in March 1987, we placed wooden nest boxes along tidal creeks in swamp forest on and near Presquile National Wildlife Refuge (37° 20' N, 77° 15' W) near Hopewell, Virginia (Blem and Blem 1991, 1992, 1994). The dominant tree species were black gum (*Nyssa sylvatica*), red maple (*Acer rubrum*), and ash (*Fraxinus* sp.). Tidal amplitude in the swamp during spring tides was >1 m. Nest boxes were placed on metal poles at approximately 100-m intervals along creek banks. Box dimensions were 28 L × 9 W × 6 D cm and the entrance hole was 3.8 cm in diameter (see Blem and Blem 1991). We determined optimal nest-box sites during the first 2 years of the study (Blem and Blem 1991) and boxes were adjusted accordingly to maximize their usage by warblers. The number of nest boxes used in the study was gradually increased from 141 in 1987 to 320 in 2004.

The contents of boxes were documented 6–20 times during the breeding season each year, depending upon the demands of other investigations of reproductive output. Females were captured as they exited nest boxes, weighed to the nearest 0.1 g on a portable electronic balance, and banded with federal bands. No warbler in these analyses was weighed twice per stage, and usually not more than once during the same nest attempt. Midday (10:00–14:00 EST) masses (g) did not vary significantly with time of day (mass = $-0.04 \text{ hr} + 16.3$, $P = 0.49$, $R^2 = 0.008$, $n = 2,124$). Only midday masses were used in the following analyses. We recorded dates of first eggs and clutch sizes for those nests visited often enough that we could be certain of the timing. Clutch size throughout the study was considered to be the number of eggs present at the

onset of incubation. We converted first egg (nest start) dates into Julian days for analysis. Prothonotary Warblers generally produce two clutches each season (Petit 1989), and second clutches typically include fewer eggs (Blem et al. 1999). We therefore divided nests with eggs in two groups—"first nests," in which first eggs were laid from 25 April through 20 May, and "second nests," in which first eggs were laid after 20 May (see Petit 1989). Some of the second nests may have been replacement clutches for first nests that had been depredated, but we are certain that many of them were produced by females that had successfully fledged young (Podlesak and Blem 2001, 2002). We used 20 May as the separation date because it represents a major hiatus in laying and is the date after which few first clutches have been laid at our study site. It also was used because of the length of time necessary for Prothonotary Warblers to complete one nesting cycle (approximately 27 days) after a mean potential starting date of 24 April (Blem and Blem 1992). We divided nesting into three phases: laying (and egg formation), incubation, and feeding young. The first phase ended with the first day of incubation and included birds that were building nests as well as laying eggs. The second phase began with the first egg and ended with hatching (Fig. 1).

Feeding visits.—In 2002, we recorded feeding visits by warblers at individual boxes during first broods by means of battery-powered remote video cameras with programmable, portable videocassette recorders. We obtained >500 hr of nest-activity records at eight nests (four broods of three young and four broods of five young) on days 7 through 10. Video cameras were small and camouflaged and did not noticeably alter behavior of the warblers. Individual visits (see Figs. 2–3) were transcribed from replays of the recordings in the lab. We totaled all feeding visits made by both parents from dawn-to-dark for all 4 days. We could not accurately assess prey size from the recordings, but we did count the number of items—mostly caterpillars—that were distinctly larger than 2 cm ("large prey"), as judged by the entry hole in the nest box. Female warblers were weighed 2 days before nestlings fledged.

Analyses.—Over the 18-year period, we obtained 2,124 measurements of body mass from

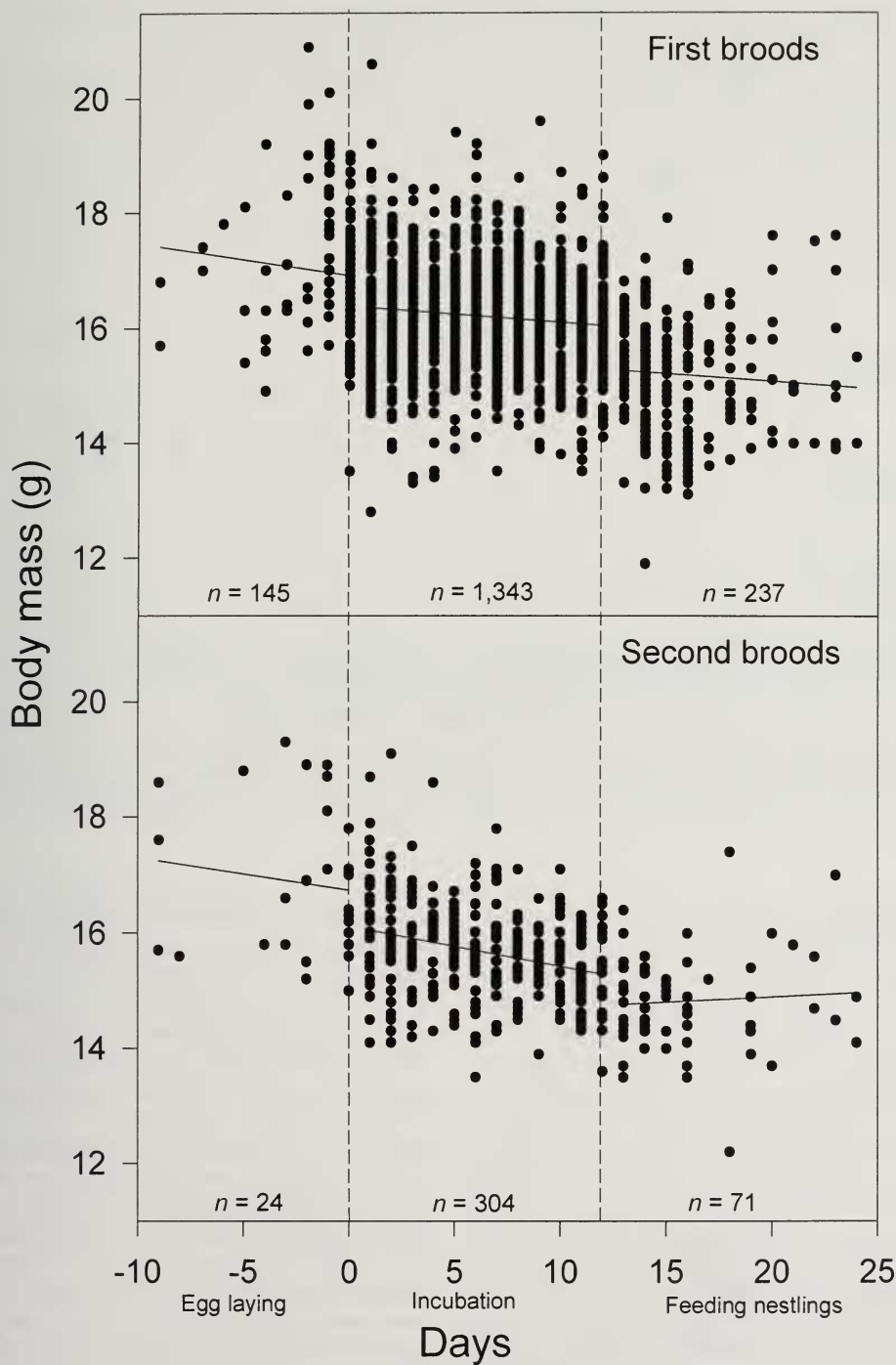


FIG. 1. Body mass (g) of female Prothonotary Warblers during nesting in eastern Virginia, 1987–2004 (day 0 = first day of incubation). Numerous circles are hidden under duplicate values ($n = 2,124$).

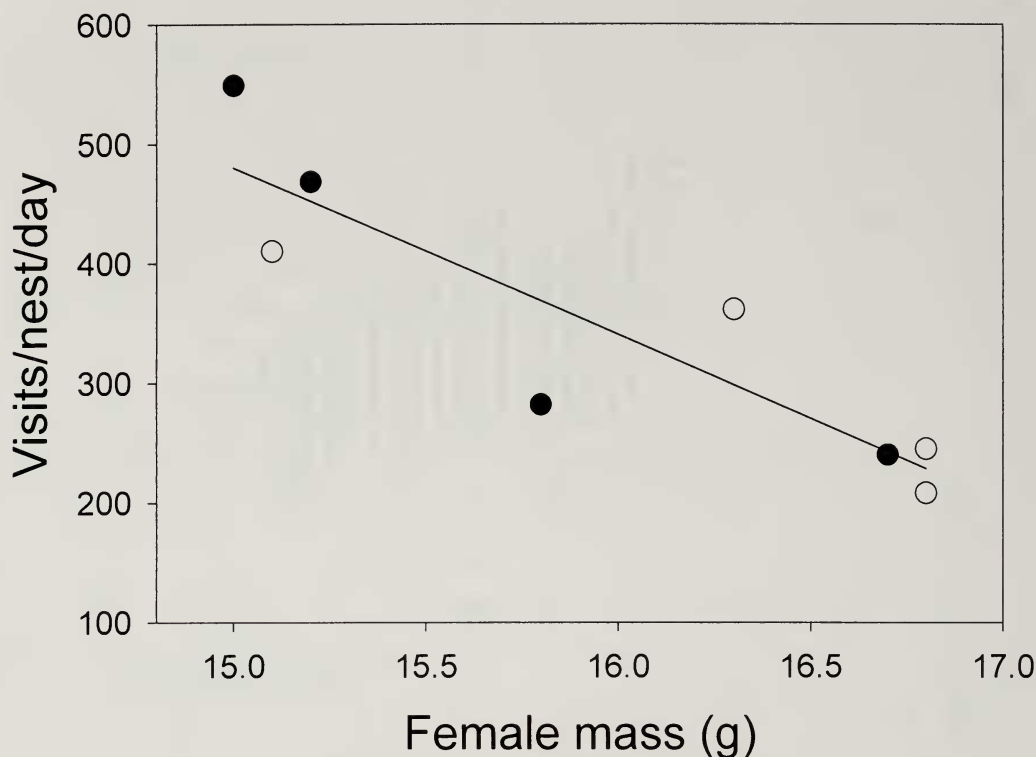


FIG. 2. Feeding visits/nest/day made by female Prothonotary Warblers during days 7–10 of feeding nestlings versus female body mass at the end of incubation, eastern Virginia, 2002. Open circles represent broods of three nestlings; solid circles represent broods of five nestlings. Nest visitation was a function of female body mass, regardless of brood size.

977 different adult female warblers. For analysis, we partitioned these measurements among nesting attempts (first and second nests, $n = 1,344$ and 780, respectively) and stages of nesting (egg formation and laying, incubating, and feeding). The number of measurements in each stage-year combination varied from 24 during laying in second nests to 1,344 during incubation in first nests. Clutch size varied from two to six eggs and ages of females ranged from 1 to 8 years.

To examine differences in mass between nests and among stages of nesting and brood sizes (adjusted for day of nesting), we used univariate ANCOVA with multiple independent variables in PROC GLM (SAS Institute, Inc. 2000). Brood size, nest attempt, age, stage of nesting, and their interactions were considered fixed (categorical) effects in various models. Day of nesting (range = -9 to 24; 0 = day of onset of incubation) was a continuous variable. Analysis of covariance

was done using the PROC GLM procedure because the data set was unbalanced among effects (Zar 1999). Type III sums of squares were used, adjusting significance of each factor for the effects of all other variables. Single comparisons of means were done by means of appropriate t -tests based on tests of equality of variances (SAS Institute, Inc. 2000). Few females were measured more than once during the same stage of nesting in a given nest in the same year; therefore, we did not use repeated measures analyses. Because some of the associated variables were not measured with each measurement of body mass, sample sizes vary among analyses. All t -tests were two-tailed. Means are presented \pm SD. Statistical significance was set at $P < 0.05$.

RESULTS

Body mass.—In the following analyses and comparisons, we assumed that patterns found between specific points along a regression

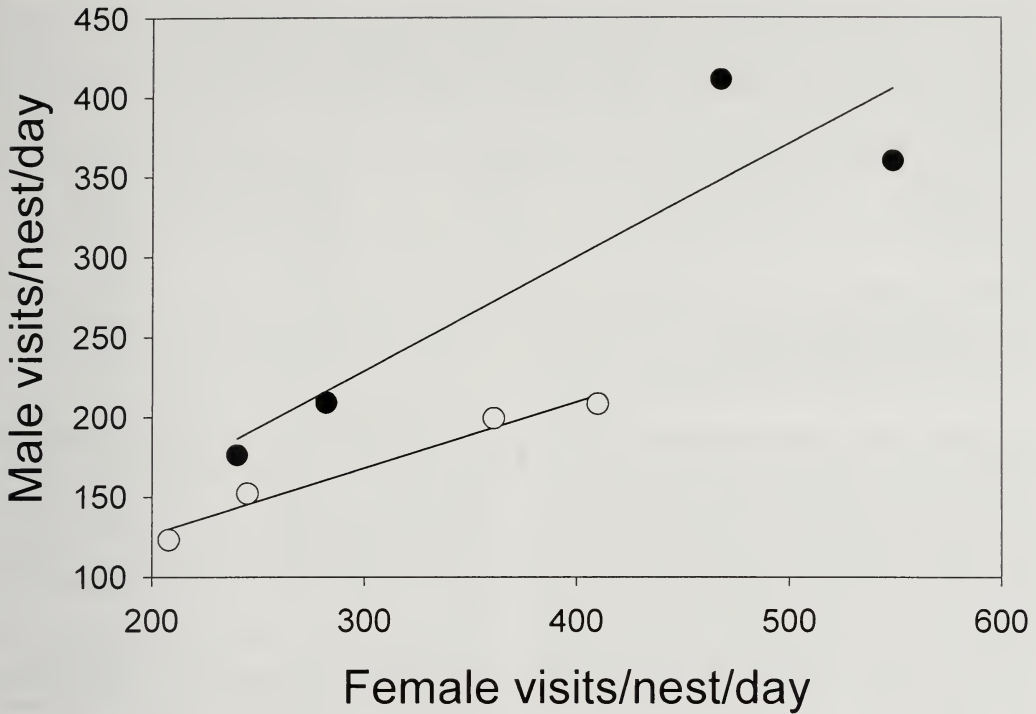


FIG. 3. Feeding visits/nest/day by mated pairs of Prothonotary Warblers during days 7–10 of feeding nestlings, eastern Virginia, 2002. Open circles represent broods of three nestlings; solid circles represent broods of five nestlings. Males brought food less often than females, but the frequency of male visits/nest/day was a function of that of females.

were representative of patterns deduced from single measurements of numerous females. This was confirmed in our observations of multiple measurements of a few single females (CRB unpubl. data).

Body mass of female Prothonotary Warblers varied over the breeding season in the typical passerine pattern. That is, variation was greatest during egg laying, mass decreased gradually during incubation, and then there was a noteworthy decrease in mass immediately after the eggs hatched (Fig. 1). After the decline immediately after hatching, adult female mass did not change over time throughout the period of feeding nestlings. Mean body masses did not differ between nest attempts during egg formation and laying (first nests: 16.9 ± 1.2 , $n = 143$; second nests: 16.8 ± 1.9 , $n = 93$, $F_{1,235} = 0.20$, $P = 0.65$), but did differ between nests during incubation (first nests: 16.2 ± 0.9 , $n = 1,225$; second nests: 15.6 ± 0.9 , $n = 304$, $F_{1,1526} = 6.7$, $P = 0.011$) and during the feeding phase (first

nests: 15.2 ± 1.0 , $n = 238$; second nests: 14.9 ± 0.8 , $n = 121$; $F_{1,358} = 6.7$, $P = 0.012$). Mass did not vary with day of nesting in the laying or feeding stages of either nesting attempt, but it did decline significantly with day of incubation (first nests: $F_{1,1342} = 18.0$, $P < 0.001$; second nests: $F_{1,303} = 33.5$, $P < 0.001$).

As judged by the collective scatter of individual masses over time, females collectively lost 10.1% of their body mass between the onset of incubation and fledging of first broods and 11.3% in second broods. Much of this loss appeared to occur during the first 2 days of feeding nestlings (5.4 and 7.7%, respectively). Mass lost during first broods was regained before the initiation of second broods. Body mass extremes were 11.9 g for an incubating bird and 21.0 g for a female during the early days of egg laying.

When the data set including all variables was considered ($n = 1,814$; Fig. 1), mass varied significantly with nest attempt, stage of nesting, clutch size (2–6), female age (1–8

TABLE 1. Analysis of covariance of body mass of female Prothonotary Warblers in eastern Virginia, 1987–2004 ($n = 1,814$). All two-way and three-way interactions were statistically insignificant except for nesting attempt \times stage of nesting. Clutch sizes were 2–6 and ages were 1–8 years. Days of nesting ranged from –9 through 24.

| Source | df | F | P > F |
|---|----|------|--------|
| Nesting attempt | 1 | 7.6 | 0.006 |
| Stage of nesting | 2 | 27.0 | <0.001 |
| Clutch size | 4 | 10.4 | <0.001 |
| Age | 5 | 6.8 | <0.001 |
| Day of nest cycle | 1 | 35.7 | <0.001 |
| Year | 17 | 2.6 | 0.015 |
| Nesting attempt \times stage of nesting | 1 | 2.8 | 0.050 |

years), day of the nest cycle, and year (Table 1). There was a significant interaction between nesting attempt (first/second nest) and stage of nesting, but no other two-way and three-way interactions were statistically significant. When stages of nesting were analyzed individually, body mass during the laying and feeding stages did not differ among clutches/broods of different sizes and mass did not vary significantly with day of nesting in these stages.

Body mass adjusted for effects of nest attempt, year, clutch size, and day and stage of nesting varied significantly with female age ($F_{1,2213} = 15.0$, $P < 0.001$; Table 2). Unadjusted masses indicated that much of this change occurred between birds in their first year (SY birds) and all older age classes (ASY). Measurements of mass were obtained from a large range of ages, including 64 measurements that exceeded the published maximum age (5 years 11 months) for the species (Kennard 1975).

During incubation, mass was significantly

TABLE 2. Least-squares means of body mass among incubating female Prothonotary Warblers during mid-incubation (days 3–8) as a function of age (years) in eastern Virginia, 1987–2004 ($n = 1,540$). All means were adjusted for the effects of nest attempt, clutch size, and day and stage of nesting.

| Age | Mean mass (g) | n |
|----------|---------------|-----|
| 1 | 16.0 | 275 |
| 2 | 16.3 | 565 |
| 3 | 16.4 | 420 |
| 4 | 16.4 | 147 |
| 5 | 16.1 | 80 |
| ≥ 6 | 16.1 | 48 |

associated with day of nesting and clutch size (Table 3). Mass tended to decrease gradually throughout incubation. Birds with larger clutches during first nesting attempts tended to have greater body mass; birds with small clutches in second nests had the lowest body mass.

Feeding visits.—Total nest visits per day made by females during days 7–10 of feeding nestlings was a function of female body mass, regardless of brood size (three young: $F_{1,3} = 13.8$, $P = 0.023$, $R^2 = 0.80$; five young: $F_{1,3} = 15.5$, $P = 0.034$, $R^2 = 0.85$; Fig. 2). Males brought food less often than females (three young: $\chi^2 = 38.2$, $df = 1$, $P < 0.052$; five

TABLE 3. Analysis of covariance of body mass among female Prothonotary Warblers in eastern Virginia, 1987–2004 by stage of nesting ($n = 2,124$ in all analyses). Clutch and brood sizes were 2–6 and ages were 1–6 years; days of nesting ranged from –9 through 24 (day 0 = first day of incubation).

| Source | df | F | P > F |
|--|----|------|--------|
| Egg formation and laying ($n = 169$) | | | |
| Nesting attempt | 1 | 0.9 | 0.34 |
| Clutch size | 4 | 2.2 | 0.092 |
| Day of nesting | 1 | 0.2 | 0.70 |
| Age | 5 | 1.7 | 0.13 |
| Incubation ($n = 1,647$) | | | |
| Nesting attempt | 1 | 52.3 | <0.001 |
| Clutch size | 4 | 9.3 | <0.001 |
| Day of nesting | 1 | 40.4 | <0.001 |
| Age | 5 | 6.3 | <0.001 |
| Feeding nestlings ($n = 308$) | | | |
| Nesting attempt | 1 | 4.3 | 0.039 |
| Brood size | 4 | 1.0 | 0.45 |
| Day of nesting | 1 | 0.3 | 0.58 |
| Age | 5 | 1.3 | 0.26 |

TABLE 4. Mean visitation rates (no./day \pm SD) of male and female Prothonotary Warblers (percent of total) for days 7–10 of nestling development in eastern Virginia, 2002.

| Brood size | Female visits | | Male visits | |
|---------------|----------------------|--------------|----------------------|--------------|
| | Per nest | Per nestling | Per nest | Per nestling |
| 3 ($n = 4$) | 306 \pm 95 (63.8) | 102.0 | 171 \pm 40 (36.2) | 57.0 |
| 5 ($n = 4$) | 396 \pm 148 (56.5) | 79.2 | 295 \pm 108 (43.5) | 59.0 |

young: $\chi^2 = 12.1$, $df = 1$, $P < 0.054$; Table 4), but frequency of male visits per day was a function of that of females (female visits = $1.0 \pm 1.06 \times$ male visits; $R^2 = 0.75$, $F_{1,3} = 17.7$, $P = 0.006$; Fig. 3). Female feeding trips per nestling decreased with brood size ($\chi^2 = 9.3$, $df = 1$, $P < 0.05$; Table 4), but male trips per nestling did not decrease ($\chi^2 = 0.034$, $df = 1$, $P > 0.05$). The percentage of total parental visits made by males declined from a high of 44.0% on day 7 to a low of 34.8% on day 10. Males brought significantly more "large prey items" to the nest than did females (males: 330, females: 210; $\chi^2 = 26.7$, $df = 1$, $P < 0.05$). These prey items were mostly *Hexagenia* sp. mayflies and lepidopteran caterpillars. There was no significant difference in the number of larger prey delivered by males to different brood sizes (175 in broods of three, 155 in broods of five; $\chi^2 = 1.2$, $df = 1$, $P > 0.05$).

DISCUSSION

Body mass clearly is associated with stage of breeding activity in small passerines (Freed 1981, Ricklefs and Hussell 1984, Cichon 2001), and each stage—egg formation and laying, incubation, and feeding of nestlings—is characterized by a different pattern of mass change (e.g., Fig. 1). Mass change of female Prothonotary Warblers in our study was similar to that reported in several other studies of passerine species (e.g., Freed 1981, Ricklefs and Hussell 1984, Johnson et al. 1990, Hillström 1995). During egg laying, body mass varied greatly with follicle formation and release of eggs, then declined progressively throughout incubation (Fig. 1), and dropped sharply at hatching. Female mass then remained relatively constant throughout the period of feeding nestlings. Mass changes in Prothonotary Warblers during egg laying and incubation were similar to those of all small passerines and require little explanation. Mass

loss at hatching is more complex and differs among species. Because the significance of this loss is uncertain, the behavior and compositional dynamics of females requires closer scrutiny.

Two potential hypotheses have been proposed to explain mass loss of female birds during feeding of nestlings: (1) energy demand (cost of reproduction hypothesis = reserve mobilization hypothesis; Cavitt and Thompson 1997), and (2) long-term benefits from reduction of power demands for flight during feeding (mass adjustment hypothesis = flight efficiency hypothesis). Forming and laying eggs, incubating, and feeding nestlings requires additional collection and expenditure of energy, whereas adjusting mass to save energy expended in flight during the numerous trips made while feeding young is an adaptive loss.

It has become obvious that body mass can vary as a result of energy demand during extreme years (Merilä and Wiggins 1997) or with larger broods (Nur 1984). It appears to be axiomatic that reserves should be depleted during times of high-energy demand and it is well known that body mass and energy reserves are closely related (Blem 1990). Part of the variation in mass within stages of the nest cycle may result from differences in annual factors, such as temperature extremes, inclement weather (Merilä and Wiggins 1997), or brood number (De Laet and Dhondt 1989). Because of our large sample size, we were able to detect annual variation within the incubation period of first nests, largely by eliminating much of the variation associated with several other variables. Others (e.g., Johnson et al. 1990) have likewise found significant annual variations in mass of breeding birds, and extreme environmental conditions in exceptional years have important influences on body mass (Merilä and Wiggins 1997).

Not all studies, however, have shown that energy demand is an important factor in body

mass. For example, larger broods are not always associated with greater mass loss of females (Pinkowski 1978, this study), even though energy expenditure by females increases with brood size (Sanz et al. 1998). Furthermore, food-supplementation studies have provided mixed results. Food supplements did not affect female mass, brood mass, or length of the nestling period among House Wrens (*Troglodytes aedon*; Cavitt and Thompson 1997) or Northern Wheatears (*Oenanthe oenanthe*; Moreno 1989a). However, food-supplemented female Mountain Bluebirds (*Sialia currucoides*; Garcia et al. 1993) maintained greater body mass and fledged larger young than females receiving no food supplementation. Some studies have found that female mass is a negative function of brood size (Nur 1984, Merilä and Wiggins 1997), and that energy demand during first broods may influence the probability of having a second brood in some species (De Laet and Dhondt 1989). In Prothonotary Warblers, it appears that many females totally recover lost mass fairly quickly between nest attempts. It has been suggested that species breeding in different environments may respond differently to stress associated with increased energy requirements and there may not be selection for adaptive mass loss (Cavitt and Thompson 1997).

The pattern of mass change in female Prothonotary Warblers in our study does not support the cost of reproduction hypothesis, but it does support the mass adjustment hypothesis. Important supporting observations included (1) the regular loss of mass after hatching in both nesting attempts, (2) the lack of influence of brood size on female mass, (3) no increasing loss in female mass as young grew and when feeding activity levels were greatest, (4) more feeding trips made by females that weighed less, and (5) little evidence that males adjusted their feeding efforts to offset demands on females. Trivers (1972) predicted that, within breeding pairs, females would provide the largest proportion of nestling care because they had a larger share of investment of energy than males. In our study, female Prothonotary Warblers made more feeding trips than males (both broods). Male Prothonotary Warblers, however, brought a greater proportion of large prey, which may have sig-

nificantly offset female effort during later stages in the nesting cycle even though males made fewer trips as nestlings neared fledging.

The mass adjustment hypothesis suggests that birds benefit from mass loss due to decreased wing loading (e.g., Freed 1981, Norberg 1981, Ricklefs and Hussell 1984, Cavitt and Thompson 1997). Energy saved by mass reduction may enable parent birds to raise more young faster or produce fledglings with greater mass. Observations supporting the mass adjustment hypothesis include (1) greater loss of mass before the period of maximum energy requirement (e.g., Freed 1981, Ricklefs and Hussell 1984, Merkle and Barclay 1996, this study), (2) loss of mass independent of brood size (e.g., Freed 1981, this study) or length of incubation (Sanz and Moreno 1995, this study), and (3) no increase in body mass among food-supplemented females feeding nestlings (Cavitt and Thompson 1997). In our study, mass loss of females during incubation was correlated with clutch size, but mass of females feeding nestlings was not affected by brood size, nor did female mass decrease throughout nestling development. If increased energy demand is important, then female mass should decline significantly as nestlings grow, although it is possible that males may "pick up the slack." That is, male warblers might feed young more frequently or with higher-quality food in large broods than small, thus reducing energy demands on females and allowing them to maintain their mass and fitness. Our observations weakly support these ideas. Males did bring more large prey items than females, but this did not vary with brood size or with nestling age. Furthermore, males made fewer visits late in the nesting cycle than females. This pattern is nearly identical with that documented for Willow Tits (*Poecile montanus*; Rytkönen et al. 1996). Similar studies have shown that nest visitation rates may be greater in males of some species (Grundel 1987), greater in females of others (Pinkowski 1978, Conrad and Robertson 1993), or may not differ between the sexes (Best 1977, Knapton 1984, Omland and Sherry 1994). The significance of the age:body mass relationship during the reproductive period is not clear. We are aware of few studies that have demonstrated an age effect on mass (see De Laet and Dhondt 1989, Merilä and

Wiggins 1997). In our study, however, female age had a significant effect on body mass, even after mass was adjusted for the effects of many other variables.

Mass variation of female birds during nesting obviously is a complex phenomenon. Deeper insight into mass variations will be obtained only with studies that combine measures of body composition, condition of reproduction tracts, and measures of hormone levels with stage of nesting. While time-consuming, collecting large data sets over numerous years is well worth the trouble, but would be even more valuable if simultaneous studies could be carried out at several sites over the range of the species.

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